NEW GENERA AND COMBINATIONS IN BRYACEAE (BRYALES, MUSCI) FOR NORTH AMERICA

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ABSTRACT

The genus *Ptychostomum* Hornsch. is resurrected for species of *Bryum* in sections *Amblyophyllum* and *Caespitibryum*, with 32 well established species found in North America transferred. The section *Leptostomopsis* of *Brachymenium* is raised to generic rank, with the one species found in North American transferred. The genus *Plagiobryoides* is newly described for the neotropical *Bryum incrassatolimbatum*. Two species of *Mielichhoferia* in North America, *M. macrocarpa* and *M. tehamensis*, are transferred to the neotropical genus *Haplodontium*.

Key words: mosses, North America, Bryaceae, *Haplodontium*, *Plagiobryoides*, *Ptychostomum*

Introduction

A considerable amount of new research has been published recently on the Bryaceae, and in particular the genus *Bryum* (Cox & Hedderson 1998, 2003; Cox *et al.* 2000; Pedersen 2002; Pedersen & Hedenas 2002; Pedersen *et al.* 2003; Spence 1987, 1996; Spence & Ramsay 1996, 1999, 2002). *Bryum* is an extremely large and diverse genus, united primarily by plesiomorphic sporophytic characters found throughout the Bryalean alternate-diplolepidous taxa (cf. Pedersen *et al.* 2003). Although there is considerable morphological variation within the genus, no attempts have been made to divide *Bryum* into smaller and presumably more natural groups. To date, the various phylogenetic studies using chloroplast DNA sequences and

morphology have not converged on a particular taxonomic solution, other than indicating that *Bryum* and the related genus *Brachymenium* are polyphyletic.

Although trying to understand the relationships among various proposed genera, species and sections of *Bryum s.l.* seems at times to be hopeless, I believe that it is possible to define natural groups within the genus based on a combination of characters from both generations. Dr. Helen Ramsay and I, while monographing *Bryum* for the Flora of Australia (Spence & Ramsay 2005), have identified groups among the gametophytic diversity in the genus. We have focused primarily on characters of the gametophyte generation, as all work to date suggests that the capsule orientation and peristome features, traditionally used to delimit genera in the family, are not indicative of evolutionary relationships above the species or perhaps sectional levels. We feel that restricting analysis to primarily gametophyte characters provides a valuable and relatively stable basis for the delimitation of natural groups (genera) in the Bryaceae (*cf.* Zander 1993 for an analogous situation in the Pottiaceae). There are several implications of our work and other studies based on DNA characters, which are discussed below.

Our work clearly supports the presence of two major lineages within *Bryum*, in addition to several smaller groups. Interestingly, these two major groups receive at least partial support from the other DNA and morphological studies cited above (*cf.* Pedersen et al. 2003). One lineage includes the many traditional *Bryum* species first grouped as the informal "Cernuibryum" by one of us (Spence 1987), along with *Acidodontium*, *Brachymenium* section *Brachymenium*, *Rhodobryum* and *Rosulabryum*. The second lineage includes the numerous small gemmiferous species of *Bryum* in sections *Bryum*, *Apalodictyon*, *Alpiniformia*, and *Doliolidium*, along with *Anomobryum* and *Brachymenium* sect. *Dicranobryum*. We have pointed out that true *Bryum* (*e.g.*, *Bryum argenteum*) is closely related morphologically to *Anomobryum*, and could easily be accomodated in that genus (Spence & Ramsay 2002). However, E.G. Britton lectotypified the genus *Bryum* with *B. argenteum*, which we regard as an unfortunate choice (Spence & Ramsay 1999). *Anomobryum,* and the type of *Bryum* are

sufficiently distinct from other members of the genus to warrant generic status. There are two potential taxonomic implications of this lectotypification if revisions are attempted. The first is that *B. argenteum* and its allies could be treated as a genus closely related to *Anomobryum*, with all other *Bryum* species given a new name. The second is that the two taxa might be combined, in which case a new name would still have to be found for all other *Bryum* species. For Australia, we chose the latter of the two (Spence & Ramsay 2002). We also argued for the conservation of the name *Bryum* with a new type, for which we selected the first species in Hedwig, *B. caespiticium* (Spence & Ramsay 1999). However, the Bryophyte Committee on Nomenclature rejected our proposal (ZijIstra 2002), based in part on a concern for the use of *Bryum caespiticium* as the conserved type, and also because further studies on *Bryum* were pending. Some of these presumed studies have now been either published (*e.g.,* Pedersen et al. 2003) or are cited in Pedersen (2002), and as noted above they do not agree with each. This leaves two choices, continue to treat *Bryum* in a very broad sense, knowing full well that it is polyphyletic, as Ochi (1992) chose to do, or come up with a new classification of the genus based on the evidence to date from all studies, both genetic and morphological. The first approach is unacceptable, so this paper as well as the treatment in Spence & Ramsay (2005) represents the first attempt since Fleischer and Brotherus (1925) to generically re-classify *Bryum*

Perhaps not surprisingly, the 19th century also witnessed confusion with the exact delimitation and nature of *Bryum*. Hedwig (1801) included a variety of species in his concept of the genus, many of which now reside elsewhere. Fairly soon thereafter both Hornschuch (1822) and Bridel (1826) described new genera long since synonymized under *Bryum*. In Hornschuch's case, it was *Ptychostomum*, described for several species now residing in *Bryum*, including *B. algovicum* and *B. uliginosum*. Bridel published *Cladodium* for the species *B. marratii* and *B. inclinatum* (=*B. amblyodon*). Most of the other species they included in these new genera have since been transferred to *Pohlia*, *Mnium* and other genera.

Validly Published Name	Year	Current Name
C. calophyllum (R. Br.) Brid.	1826	*Bryum calophyllum*
C. demissum (Hook.) Nees	1836	*Plagiobryum demissum*
**C. inclinatum* (Sw. ex Brid.) Brid.	1826	*Bryum amblyodon*
C. rhamphostegium Hampe	1865	*Acidodontium rhamphostegium*
C. socorrense Hampe	1869	*Bryum limbatum*
C. uliginosum Brid.	1827	*Bryum uliginosum*

Table 1. Summary of validly published species of *Cladodium* Bridel, year of publication, and currently accepted name. The lectotype species is indicated by an asterisk.

For some reason, these generic names never caught on with later bryologists, and have languished under *Bryum* ever since, probably because the first species of *Bryum* in Hedwig (1801), *B. caespiticium*, is morphologically similar to both *B. algovicum* and *B. amblyodon*. All those species still remaining in *Bryum* that were placed by these two in *Cladodium* and *Ptychostomum* are in the informal group "Cernuibryum" while *B. argenteum* is in the group "Bryum" of Spence (1987).

Because of the above considerations, I propose here to re-instate the genus *Ptychostomum* Hornschuch for those species of *Bryum* in the informal group "Cernuibryum" of Spence (1987). Since all three species first cited by both Bridel and Hornschuch are related, either genus could be used, but *Ptychostomum* has priority over *Cladodium* by four years. Interestingly, my work also suggests two closely related groups within *Ptychostomum*, one corresponding to the species *B. algovicum*, and the second to those species related to *B. uliginosum*. For now I prefer to keep these two groups together, although future work may indicate that they represent distinct but closely related genera. The studies of Cox and Hedderson (2001) and Pedersen *et al.* (2003) both show a well supported clade that consists of species in *Ptychostomum*, although including the species *Bryum donianum*, which based on its gamteophyte may be a *Rosulabryum*.

Validly Published Name	Year	Current Name
P. caespiticium Brid.	1827	*Bryum algovicum*
**P. cernuum* (Hedw.) Hornsch.	1822	*Bryum uliginosum*
P. compactum Hornsch.	1822	*Bryum algovicum*
P. pendulum Hornsch.	1822	*Bryum algovicum*
P. puchellum R. Br.	1823	*Bryum algovicum*
P. radiculosum Brid.	1826	*Bryum uliginosum*

Table 2. Summary of validly published species of *Ptychostomum* Hornsch., year of publication, and currently accepted name. The lectotype species is indicated by an asterisk.

Tables 1 and 2 list all validly published species in *Cladodium* and *Ptychostomum*. Pfeiffer (1873) lectotypified *Cladodium* with the species *C. inclinatum*, but *Ptychostomum* has not yet been lectotypified. Hornschuch's understanding of the genus was based on certain characters of the sporophyte, primarily the peristome. His essential characters included *"Peristomium duplex: exterius dentibus sedecim erectis, interius membrana hyalia plicata, peristomio externo adhaerens et denta ejusdem inter se conjungens"*. The adherence of the endostome to the exostome is a critical character in the circumscription of the genus. The two species Hornschuch included in *Ptychostomum* are currently known as *Bryum algovicum* and *B. uliginosum*. Both these species are characterized by reduced peristomes with the endostome adherent to the exostome. I have selected *P. cernuum* (=*B. uliginosum*) as the lectotype because *P. pendulum* (=*B. algovicum*) is closely related to the type of *Cladodium*, *C. inclinatum*. This selection was made in the interests of preserving both generic names, in case *Cladodium* is also recognized at the generic level at some point in the future. *Ptychostomum cernuum* is in a different section than *C. inclinatum* and is not closely related to it.

Ptychostomum Hornsch., Flora 5, 2: syll. 62, 1822. Lectotype species: *Ptychostomum cernuum* Hornsch., Flora 5, 2: syll. 64, 1822. In addition, Hornschuch included the species currently known as *Bryum algovicum* (Brid.) B.S.G. in the genus as *Ptychostomum pendulum* Hornsch., Flora 5, 2: syll 62, 1822.

The following 27 species found in North America are also transferred to the genus.

Ptychostomum archangelicum (B.S.G.) J.R. Spence, **comb. nov.**
Basionym: *Bryum archangelicum* B.S.G., Bryol. Eur. 4: 153, 1846.

Ptychostomum arcticum (R. Br.) J.R. Spence, **comb. nov.**
Basionym: *Pohlia arctica* R. Br., Chlor. Melvill. 38. 1823.

Ptychostomum badium (Brid.) J.R. Spence, **comb. nov.**
Basionym: *Bryum caespiticium* var. *badium* Brid., Bryol. Univ. 1: 850. 1827.

Ptychostomum bimum (Schreb.) J.R. Spence, **comb. nov.**
Basionym: *Mnium bimum* Schreb., Bot. Zeit. (Regensburg) 1: 79. 1802.

Ptychostomum calophyllum (R. Br.) J.R. Spence, **comb. nov.**
Basionym: *Bryum calophyllum* R. Br., Chlor. Melvill. 38. 1823.
Synonym: *Cladodium calophyllum* (R. Br.) Brid., Bryol. Univ. 1: 620. 1826.

Ptychostomum cryophilum (Mårt.) J.R. Spence, **comb. nov.**
Basionym: *Bryum cryophilum* Mårt., K.V.A. Afh. Natursk. 15: 183, 1956. Nom. nov. *B. obtusifolium* Lindb., Ofvers. Forh. Konsch. Svenka Vetensk.-Akad. 23: 544. 1866; not *B. obtusifolium* Brid., Muscol. Recent 2(3): 52. 1803.

Ptychostomum curvatum (Kaur. & Arn.) J.R. Spence, **comb. nov.**
Basionym: *Bryum curvatum* Kaur. & Arn., Bot. Not. 67. 1897.

Ptychostomum cyclophyllum (Schwaegr.) J.R. Spence, **comb. nov.**
Basionym: *Mnium cyclophyllum* Schwaegr. Sp. Musc. Suppl. 2, 2(2): 160, pl. 194. 1827.

Ptychostomum inclinatum (C. Muell.) J.R. Spence, **comb. nov.**
Basionym: *Cladodium inclinatum* (Sw. ex Brid.) Brid., Bryol. Univ. 1: 620, 1826.

Ptychostomum intermedium (Brid.) J.R. Spence, **comb. nov.**
Basionym: *Pohlia intermedia* Brid., Muscol. Recent 2(3): 144, pl. 2, f. 12. 1803.

Ptychostomum knowltonii (Barnes) J.R. Spence, **comb. nov.**
Basionym: *Bryum knowltonii* Barnes, Bot. Gaz. 14: 44, 1889.

Ptychostomum lonchocaulon (C. Muell.) J.R. Spence, **comb. nov.**
Basionym: *Bryum lonchocaulon* C. Muell., Flora 2(6): 90, 1819.

Ptychostomum longisetum (Bland. *ex* Schwaegr.) J.R. Spence, **comb. nov.** Basionym: *Bryum longisetum* Bland. *ex* Schwaegr., Spec. Frond. Musc. Suppl. 1, 2: 105, pl. 74, 1816.

Ptychostomum marratii (Hook. & Wils.) J.R. Spence, **comb. nov.**
Basionym: *Bryum marratii* Hook. & Wils., Bryol. Brit., p. xi (add.), pl. XXXIIb, 1855.

Ptychostomum meesioides (Kindb.) J.R. Spence, **comb. nov.**
Basionym: *Bryum meesioides* Kindb., Bull. Torrey Bot. Club 16: 95, 1889.

Ptychostomum neodamense (Itzigs.) J.R. Spence, **comb. nov.**
Basionym: *Bryum neodamense* Itzigs. in C. Muell., Syn. Musc. Frond. 1: 258. 1848.

Ptychostomum pallens (Sw.) J.R. Spence, **comb. nov.**
Basionym: *Bryum pallens* Sw., Monthl. Rev. Lond. 34: 538. 1801.

Ptychostomum pallescens (Schleich. *ex* Schwaegr.) J.R. Spence, **comb. nov.** Basionym: *Bryum pallescens* Schleich. *ex* Schwaegr., Sp. Musc. Suppl. 1, 2: 107, pl. 75. 1816.

Ptychostomum purpurascens (R. Br.) J.R. Spence, **comb. nov.**
Basionym: *Pohlia purpurascens* R. Br., Clor. Melvill. 39. 1823.

Ptychostomum reedii (Robins.) J.R. Spence, **comb. nov.**
Basionym: *Bryum reedii* Robins., Bryol. 69: 107, 1966.

Ptychostomum rutilans (Brid.) J.R. Spence, **comb. nov.**
Basionym: *Bryum rutilans* Brid., Bryol. Univ. 1: 684. 1826.

Ptychostomum salinum (Hag. *ex* Limpr.) J.R. Spence, **comb. nov.**
Basionym: *Bryum salinum* Hag. *ex* Limpr. Laubm. Deutschl. 2: 334. 1892.

Ptychostomum schleicheri (Schwaegr.) J.R. Spence, **comb. nov.**
Basionym: *Bryum schleicheri* Schwaegr., Sp. Musc. Frond. Suppl. 1, 2: 113, pl. 73 p.p. 1816.

Ptychostomum turbinatum (Hedw.) J.R. Spence, **comb. nov.**
Basionym: *Mnium turbinatum* Hedw., Sp. Musc. Frond. 191. 1801.

Ptychostomum warneum (Röhl.) J.R. Spence, **comb. nov.**
Basionym: *Mnium caespiticium* var. *warneum* Röhl., Deutsch. Fl. (ed. 2), Kryptog. Gew. 3: 95. 1813.

Ptychostomum weigelii (Spreng.) J.R. Spence, **comb. nov.**
Basionym: *Bryum weigelii* Spreng., Mant. Prim. Fl. Hals. 55. 1807.

Ptychostomum wrightii (Sull. & Lesq.) J.R. Spence, **comb. nov.**
Basionym: *Bryum wrightii* Sull. & Lesq., Proc. Amer. Acad. Arts Sci. 4: 278. 1860.

Several additional species of *Bryum* that may belong in *Ptychostomum* have been reported from North America. Most are poorly known Arctic species, and more work is needed to determine their status. These are: *B. acutiforme* Limpr., *B. axel-blyttii* Philib., *B.*

bryoides (R. Br.) Ångstr., *B. brachyneuron* Kindb., *B. hagenii* Limpr., *B. nitidulum* Lindb., *B. subneodamense* Kindb., and *B. teres* Lindb.

The following three species of *Bryum* also occur in Australia, and are transferred for the Flora of Australia (Spence & Ramsay 2005).

Ptychostomum angustifolium (Brid.) J.R. Spence & H.P. Ramsay, **comb. nov.** Basionym: *Bryum angustifolium* Brid., Musc. Recent. Suppl. 3: 31, 1817. Synonym: *Bryum caespiticium* Hedw., Sp. Musc. Frond., 1801, not *Ptychostomum caespiticium* Brid., Bryol. Univ. 1: 837, 1827.

Since the combination *Ptychostomum caespiticium* has priority as a synonym of *Ptychostomum pendulum* a new name is needed for the species known as *B. caespiticium* Hedw. The first name that still remains valid within that species is *B. angustifolium* Bridel.

Ptychostomum creberrimum (Taylor) J.R. Spence & H.P. Ramsay, **comb. nov.** Basionym: *Bryum creberrimum* Taylor, Lond. J. Bot. 5: 54. 1846.

Ptychostomum pseudotriquetrum (Hedw.) J.R. Spence & H.P. Ramsay, **comb. nov.** Basionym: *Mnium pseudotriquetrum* (Hedw.) Schwaegr., Spec. Musc. Suppl. 1, 2: 110. 1816.

Leptostomopsis (C. Muell.) J.R. Spence & H.P. Ramsay, **stat. nov.** Lectotype: *L. systylium* (C. Muell.) J.R. Spence & H.P. Ramsay, **comb. nov.** Basionym: *Bryum systylium* C. Muell., Syn. Musc. Frond. 1: 320. 1848.

The species in section *Leptostomopsis* of *Brachymenium* comprise a distinctive group that superficially resembles *Leptostomum*. They are characterized by densely compact cushions on bark or rock, dense lamina areolation, a long hyaline spinose hairpoint, and erect capsules with reduced peristomes. In an earlier paper (Spence 1996) I first suggested that the section may represent a distinct genus. The work of Cox & Hedderson (2003) and Pedersen *et al.* (2003) support this,

suggesting that the group is basal to the remainder of the Bryaceae, and only distantly related to the rest of *Brachymenium* as well as *Bryum*. This section is sufficiently distinct from other members of the Bryaceae in both genetic and morphological characters to warrant generic rank. There are about 8-10 species, pantropical and southern hemispheric in distribution in drier tropical and subtropical regions. One species, the type, is known from southern areas of the U.S.A.

Plagiobryoides J.R. Spence, **gen. nov.**

Caules uniformiter foliati. Folia ovata, in statu sicco contorta, areolatione laminali subheterogenea, cellulis distalibus brevibus irregulariter subquadratis vel brevi-rhombicis, in parte mediana atque proximali cellulis paulo longi-rhombicis, marginibus distincte limbatis valde bi-vel multistratosis, costa in sectione transversali cellulis ducum in strato unico adaxialiter supra stratum stereidarum bene effectum sitis praedita. Gemmae asexuales nullae. Plantae dioicae. Capsulae subzygomorphae, ore obliquo, inclinatae vel subrectae; peristomium diplolepidum, segmentis endostomialibus longitudine aequis exostomio, ciliis imperfectis vel nullis. Sporae parvae, 10-15 um.

Stems elongate, to 30 mm, simple, rarely branched, in transverse section with weakly developed central strand, with large thin-walled cells exterior, and somewhat smaller and thicker-walled peripheral cells; evenly foliate; rhizoids abundant, red-brown, papillose. **Leaves** pink, red to brown, ovate, keeled, contorted and twisted when dry, spreading when wet, concave, 1.0-2.5 mm long, apex acute to obtuse, moderately to strongly and longly decurrent; costa broad, strong, not reaching apex to rarely percurrent, in cross-section with enlarged guide-cell like layer, one to two-layered, ventral to a well developed stereid band, sometimes guide-like cells lacking; lamina areolation somewhat heterogenous, thin-walled, with short irregularly subquadrate to short-rhomboidal cells distally and somewhat longer irregularly rhomboidal cells in median and proximal part, typically, 60-100 μm x 12-30 μm wide, margins with strongly differentiated border, bi- to multistratose, of thick-walled cells. **Specialized asexual gemmae** lacking. **Sexual condition** dioicous. **Seta** slender, flexuose to

bent near base. **Capsules** suberect, somewhat zygomorphic and asymmetric with oblique mouth, apophysis slender, well differentiated, operculum conic, without apiculus, peristome double, exostome teeth lanceolate, somewhat united at base, yellowish, basal membrane hyaline, high, segments slightly keeled, with narrow perforations or slits, the same length as exostome, cilia rudimentary or lacking. **Spores** small, 11-14 um (description of sporophyte from Ochi and Salazar-Allen 1990).

Type species: *Plagiobryoides incrassatolimbata* (Card.) J.R. Spence, **comb. nov.** Basionym: *Bryum incrassatolimbatum* Card., Rev. Bryol. 36: 114, 1909.

Plagiobryoides incrassatolimbata is a distinctive species that cannot be confused with any other member of the Bryaceae. The extremely lax lamina areolation and often multistratose limbidium are diagnostic. Remarkable for the family, lamina cells near the leaf tip are often nearly isodiametric to subquadrate. The capsule is similar to that found in *Plagiobryum* and its allies in the broad sense, including *Bryum cellulare* and related species. This distinctive plant is found on wet calcareous rock and is a Neotropical species, distributed from the southwestern U.S.A. through Mexico and Central America.

Haplodontium Hampe

Haplodontium consists of species with lateral sporophytes and an extremely reduced peristome, typically of one layer. Shaw (1985) transferred all species in the genus to *Mielichhoferia* Hornsch. However, the recent work using DNA analysis (Cox and Hedderson 2003; Cox et al. 2000; Pedersen 2002; Pedersen and Hedenas 2002; Pedersen et al. 2003) indicates that the type of *Mielichhoferia*, *M. mielichhoferiana*, is more closely related to *Pohlia*, while many other species originally in *Haplodontium* are deeply nested with the Bryaceae. These include the two North American species *M. macrocarpa* and *M. tehamensis*, which are gametophytically very close to other species of *Haplodontium* and *Plagiobryum*, and very similar to

the type of the genus, *H. megalocarpum* Arnott. These two species are thus transferred to a resurrected *Haplodontium* as:

Haplodontium macrocarpum (Hook. *ex* Drumm.) J.R. Spence, **comb. nov.** Basionym: *Weissia macrocarpa* Hook. *ex* Drumm. Musci Amer., Brit. N. Amer. 74. 1828.

Haplodontium tehamense (Showers) J.R. Spence, **comb. nov.** Basionym: *Mielichhoferia tehamensis* Showers, Bryol. 83: 365, 1980.

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